1993

Mechanisms of succession in a carrion community : a fourteen day post mortem study

Charles Dean Franklin
San Jose State University

Order Number 1354143

Mechanisms of succession in a carrion community. A fourteen day post mortem study

Franklin, Charles Dean, II, M.A.

San Jose State University, 1993

U·M·I
300 N. Zeeb Rd.
Ann Arbor, MI 48106

MECHANISMS OF SUCCESSION IN A CARRION COMMUNITY.
A FOURTEEN DAY POST MORTEM STUDY

A Thesis

Presented to

The Faculty of the Department of Biological Sciences

San Jose State University

In Partial Fullfillment

of the Requirements for the Degree

Master of Arts

by

Charles Dean Franklin II

August, 1993

APPROVED FOR THE DEPARTMENT OF BIOLOGICAL SCIENCES

Ronald E. Stecker

Dr. Ronald E. Stecker

William E. Bros

Dr. William E. Bros

Dr. Michael Kutileck

APPROVED FOR THE UNIVERSITY

Serena N. Stanford

Abstract

Mechanisms of Succession in a Carrion Community.
A Fourteen Day Post Mortem Study

by Charles Dean Franklin II

This thesis addresses the topic of the mechanisms of succession in a carrion community during the first fourteen days post mortem. The focus of this thesis is to examine the affects of disturbance on the sequence of succession and species composition. Individual species were examined as well as overall species composition. In addition, temperatures were measured to analyze the affect of temperatures on the carrion community.

Species compositional change, day to day, was affected by disturbance. However, disturbance did not cause significant changes in overall species composition in the first fourteen days post mortem. Community development, based on the research in this study, was unpredictable when disturbances occurred. Environmental temperatures were not related to core temperatures, and core temperatures did not relate to overall species composition.

Acknowledgments

I would like to thank Dr. William E. Bros for his considerable help in the design, writing, and evaluating of this thesis. Also I would like to thank Drs. Michael Kutileck and Ronald E. Stecker for their evaluation of this thesis.

To the following people I am eternally grateful for their individual contributions with regard to this project: John Baird, for allowing me to use his property to conduct my research; Earl Yorkey for helping place my pigs after they were dead, and for the set up and breakdown of the cages and rotting corpses; Dan Gross for fly identification; Dr. Curtis Sabrosky for the identification of the Chloropidae; Dan Verity for the identification of the Histeridae; and for Dr. J. Gordon Edwards for his help in identification of the rest of the insects. I wish to express my gratification to my family, especially my mother, Marilyn Franklin, for tolerating the flies in the bathroom during the two weeks of my research and the unpleasant odors in the backyard during the rearing phase of my project.

Table of Contents

Section	Page
Introduction	1
Material and Methods	4
Results	7
Discussion	10
Literature Cited	14

Tables	Page
Table 1. Multivariate analysis of variance for treatment, time and location effects for four species of blow fly.	17
Table 2. Three-way analysis of variance for treatment, time and location effects for *Eucalliphora lilaea*.	18
Table 3. Three-way analysis of variance for treatment, time, and location effects for Compsomyiops calipes.	19
Table 4. List of species collected from carrion. Stages of decay listed.	20

Figures	Page
Figure 1. Three-way analysis of variance for treatment showing density of *Eucalliphora lilaea* .	21
Figure 2. Multivariate analysis of variance for time affect showing mean abundance for *Eucalliphora lilaea* and *Compsomyiops calipes*.	22
Figure 3. Czechanowski's Quantitative Similarity showing species composition between successive days over time for three treatments: traumatized, whole-body (control), and off-ground.	23

Introduction

Facilitation (Connell and Slayter, 1977) involves a predictable sequence of succession where early colonizers alter a habitat, thereby allowing the colonization of later arriving species. Forensic entomology relies on this predictable sequence to help determine the post mortem interval in medicolegal cases. Even if the facilitation model is correct, the exact sequence and timing may be unpredictable because forensic entomologists have found that disturbance and environmental factors can either enhance or inhibit the succession sequence (Catts et al., 1992, 1990). To help alleviate uncertainty in determining the post mortem interval, forensic entomologists have defined stages of decay associated with this predictable sequence (Tullis and Goff, 1987; Early and Goff, 1986; Payne, 1965; Bornemissza, 1957).

Stages of decay help to define the time of colonization of species common in facilitation. However, community development may not always follow this predictable model. For example, Schoenly (1987) states that the stages of decay, when used alone, contain inadequacies that can create error in summarizing patterns of faunal succession. He concluded that, "the carrion arthropod community develops primarily as a continuum of gradual change: rapid at first, slow during peak activity, and erratic in the final days as carcass resources become depleted" (Schoenly, 1987). Because the conditions under which a community develops may be misleading and unpredictable, Connell and Slayter (1977) proposed two other models to define this unpredictable community development: tolerance and inhibition.

In the tolerance model, species may be present in low numbers early on, or remain dormant (e.g., seed banks) throughout community development. The importance of any species at any point in development is determined by environmental conditions; when conditions for that particular species are optimum, they become more abundant. Lane (1975) found that photo period, temperature, and humidity affected the abundance of visiting flies, and that certain flies initiated activity earlier in the day than other species. Spight (1977) found that certain tropical gastropod communities contain many habitat generalists whose activities of development and survival are restricted by a wide range of environmental variables. The timing and predictability of the developmental sequence would be a function of the timing and predictability of environmental conditions as well as the individual life histories of each species.

In the inhibition model, early colonists maintain dominance and resist invasion until a disturbance event reduces their numbers. Disturbances are heterogeneous in time and space and generate patches in natural systems (Sousa, 1979). When a disturbance occurs, new resources are exposed. In this model, the developmental sequence depends on the timing and severity of disturbance along with the availability of potential colonists at the time of disturbance. For example, Hemphill and Copper (1983) found that disturbance initiates successional changes by eliminating competitive dominants, allowing other species to colonize. Kneidel (1984) found that one species of blow fly, *Phaenicia caeruleiviridus*, was competitively superior on small mammal carrion and that in carrion not occupied by this species, several other species were able to colonize.

If forensic entomologists are to rely on the predictability of community development to determine time of death, it is vital to understand how disturbances and environmental factors may alter the sequence and timing of community development. In the present study, three factors were examined in relation to their potential influence on post mortem community development in pig carcasses: trauma, environmental temperatures, and the presence or absence of soil fauna.

Trauma

Trauma is an injury caused by an extrinsic agent. Trauma in carrion results in a break in the integument from knife or gunshot wounds (Catts, 1992) and may alter the succession sequence. Species previously unable to colonize may now occupy and utilize the newly exposed resources.

Environmental temperatures

Environmental temperatures play a role in the timing of successional stages. Pfunter (1977) found that of three blow fly species present on carrion, *Eucalliphora lilaea* was more abundant at temperature regimes between 17^0 C and 20^0C. Deionier (1940) found that at lower temperatures blow fly activity was reduced, and carcasses did not become infested for several days following death. Johnson (1975) concluded that the colder temperatures altered the decomposition process of carrion due to the absence of insects.

Presence or absence of soil

The soil contains species of invertebrates that may directly influence development of the carrion feeders and contribute to the decomposition process (Bornemissza, 1957). Beetles, namely the *Histeridae* and *Staphylinidae*, are predatory and parasitic and have an effect on larval development (Payne, 1965; Early and Goff, 1986).

Bornemissza (1957) found that decomposition products, which passed into the soil during the various stages of decomposition, adversely affected the soil, the plants present, and the associated fauna.

Pig carcasses were used in the present study because they may be easily manipulated. Also, the patterns of arthropod succession do not differ significantly between pig carcasses that had moderate weight differences (Hewadikaram and Goff, 1991). N.H. Haskell (1989, unpublished data), made a comparative study between the rates of decomposition between adult and infant humans remains and the pig model. His results showed that the species composition between the different models did not differ, but the rate of decomposition was governed by the amount of carrion available (Catts and Goff, 1992).

Materials and Methods

The study was conducted in San Bruno Canyon located between Morgan Hill and South San Jose, Ca. This area is surrounded by hills and contains a 730 hectare private pasture land. Sparse oak trees and a creek bisect the pasture occupied by 300 head of cattle.

To test the three possible mechanisms of succession, three treatments were used: trauma, whole-body, and off-ground. To simulate trauma, a 25 cm incision was made into the abdominal cavity of one set of pigs. The incision caused a break in the integument, and evisceration occurred. These newly exposed resources early on were used to examine how disturbance affects successional sequence and species composition. One set of pigs, left alone, served as the control. To determine the effects of soil on species composition and successional sequence, one set of pigs was suspended 25 cm above the ground on a steel wire platform.

Changes in species composition were measured with random collections of larvae taken daily from three pigs with a 2.5 cm X 7.6 cm plastic cylinder. Larvae of the first week were reared in 2 liter ice cream containers with 10 cm of soil and approximately 3 grams of beef liver. The liver was replaced as necessary. The second week's larvae were submerged in boiling water and placed in 75% ethanol for preservation after death. Upon emergence, the first week's adult flies were identified to species (James, 1955) and counted. Larvae of the second week were counted according to instar present and identified to species (Knipling, 1939).

A multivariate three-way analysis of variance (Tabachnick and Fidell, 1989) was used to test differences in species composition with regard to treatment, location, and time. Four species of blow fly, family Calliphoridae, were tested: *Eucalliphora lilaea* (Walker); *Compsomyiops calipes* (Dear); *Phormia regina* (Meigen); *Calliphora vomitoria* (Linneaus). Three different treatment levels were used: trauma, whole-bodied, and off-ground. Two locations within each treatment were examined: natural orifices and abdominal-traumatized areas. Two time regimes were analyzed: week one and week two. To avoid a Type I error, the alpha was set at 0.025. Significant multivariate interactions with time and treatment (i.e., treatment*location*time or treatment*time) would show that species compositional change depends upon disturbance.

A three-way analysis of variance (Zar, 1984) was used to test abundance changes in individual species. Significant interactions with treatment and time would show that abundance of a particular species at any time is affected by treatment.

Czechanowski's Quantitative Similarity Index (Field and Mcfarlane, 1968; Bray and Curtis, 1957) was used to determine if succession progressed continuously or occurred as discrete species turnover. If the similarity of species was continuous, then succession would not result in species turnover. Discrete species turnover would result in one or more species changing as time progressed. If the similarity over time was constant, then the mechanism of succession is consistent, with the value of similarity directly related to the rate of change between two successive days. If it is disjunct, the distance between the peaks or valleys is a measure of length of identifiable stages.

The effect of temperature on species composition, environmental temperatures, was measured with maximum/minimum thermometers placed at each site. A mercury thermometer was inserted approximately 20 cm into the anus of each pig to measure the effect of environmental temperature on internal core temperature of carrion. The effect of environmental temperature on the soil directly beneath the carrion was examined daily by placing a soil thermometer underneath each pig. All temperatures were recorded once daily for the first ten days. Collapse of the anal tissues by larval activity in several pigs prevented accurate core temperature measurements after 10 days.

Correlation analyses were used to test the relationship between external and internal temperatures. Strength of potential relationships was measured with the Pearson Product Moment Correlation Coefficient (Zar, 1984). A high correlation between environmental and core temperatures would indicate that environmental temperatures directly affect the internal core temperatures. A low correlation between environmental and core temperatures would show that temperatures are independent of each other and that internal core temperatures rise solely as a result of the natural decay process. Also, soil temperatures directly underneath the pig carcass would not be affected by environmental factors, and would remain stable.

To analyze the mechanisms of succession on the carrion community, nine pigs between 50 and 65 lbs were sacrificed on site using a single bullet to the head. Three pigs were used for each of the three treatments: trauma, no soil contact, and the control. Each pig was placed into a 152 cm X 152 cm X 76 cm cage with 3 cm X 5 cm mesh wire after death ensued. Chicken wire was placed over the top to prevent vertebrate scavengers. The site for each cage was randomly selected within a 730 hectare pasture. Adjacent sites were not permitted, however, because they might influence each other.

Observations were made once a day, at random times, from February 10, 1990 to February 23, 1990. Each pig was randomly selected to prevent biased visitation. Observations of the pigs noted general conditions, larval activity, insect activity, temperature readings, and weather data. Three random sites were selected for collection over each day. Larvae were collected by scooping a larval mass with a 2.5 cm X 7.6 cm plastic cylinder. Adults were collected with net sweeps over each randomly selected pig. Insect sweeps were not made when winds increased to 8 knots.

Results

The insignificant multivariate interactions showed that species compositional change does not depend on the combination of treatment, location, and time (Table 1). Disturbances or location did not affect species compositional change, and only time affected the change in composition (p=0.010). The minimum detectable difference for this test is 10.2, and the grand mean is 56.25. This shows that the experimental design was capable of resolving a 20 percent difference from the grand mean.

The significant 3-way ANOVA showed that disturbance affects the abundance of *Eucalliphora lilaea* (Table 2). The significant treatment effect (p=0.018) and the *a priori* test showed that the abundance of *E. lilaea* was greatest on traumatized pigs (Figure 1). However, the proportion of the *E. lilaea* population on traumatized pigs vs. non-traumatized pigs is not affected by time as indicated by the non-significant treatment * time interaction.

Time affects the abundance of *E. lilaea* (Table 2) and third instar *Composmyiops calipes* (Table 3). The significant time effect (p=0.010) shows that *E.lilaea* was the most abundant fly species throughout the first week (Figure 2). The abundance of third instar *C. calipes* is greatest during the second week (p= 0.02) and was almost nonexistent during the first week (Figure 2). Abundance over time was not affected by treatment as indicated by the insignificant treatment and treatment * location/time interaction. Note that location and time were not significant. This interaction is based solely on the location of samples taken at a particular time interval. The primary component of species compositional change was a function of two species. *Phormia regina* and *Calliphora vomitoria* showed no significant change throughout the entire study.

Three species of blow fly had oviposited within twenty-four hours: *Calliphora vomitoria, Eucalliphora lilaea,* and *Phormia regina*. Figure 3 illustrates the highly variable populations of these three species with regard to treatment throughout the first two weeks post mortem. The high degree of similarity with traumatized pigs coincides with the significant treatment and time effects (Table 2) for *Eucalliphora lilaea* . *E. lilaea* was the most abundant fly species on traumatized pigs throughout the first week. While all three species were present through the entire two weeks post mortem, the appearance of a fourth species, *Compsomyiops calipes* , changed the species composition. *C. calipes* was the most abundant fly during the second week. The sharp decline between days six and seven in figure 3 coincides with the significant time effect for *C. calipes* (Table 3). The high variability in species composition can be attributed to a change in the population of each of the four species present over successive days. The lack of continuous phases in similarity over successive days shows that the populations of the four blow fly species were highly variable. In the case of the off-ground pigs, however, an indiscreet phase of species composition can be seen for the first 10 days. The sharp disjunctions of the off-ground pigs between days 10 and 13 signify quick colonization of species and an abrupt change in species composition.

There was no apparent relationship between internal and external temperatures for all treatments. The correlation between internal and external temperature in traumatized pigs was -0.47 and not significant (p=0.170). The correlation between internal and external temperatures in control pigs was 0.215 (p=0.550). The correlation between internal and external temperatures in off-ground pigs was 0.053, and not significant (p=.884). Soil temperatures were not correlated with environmental temperatures and ranged from 15-17°C throughout the entire study.

Discussion

The change in species composition was independent of either treatment or location. Disturbances also did not change the overall species composition. Payne (1965), Tullis et al. (1987), and Catts (1992) found that blow flies were generally the first to arrive at carrion, as in this study. Blow flies are important to the onset of decay (Johnson, 1975). The larval activity of these species helps to create changes in the carcass which allow "later-successional" species to colonize. According to Connell and Slayter (1977), the facilitation model is defined as a changing of conditions of the community by the early colonizers to allow further colonization by later arriving species. This study agrees with the facilitation model in that the blow flies changed the conditions of the carrion.

However, the similarity analysis indicated that compositional shifts were not the same between treatments for the first 6 days. In this study, two of the four blow fly species changed abundance over the first seven days. *E. lilaea* was found in high abundance throughout the first six days, abruptly replaced by *C. calipes* in the seventh day. This abrupt change in species composition may result in an unpredictable sequence throughout the first week of the post mortem interval. Deonier and Knipling (1940) found that the eggs of *C. calipes* hatch from 20-24 hours, and the larvae mature within 5 days. Similarly, Kamal (1958) found that the eggs of *E. lilaea* hatch from 14-30 hours, and the larvae mature within 12-16 days. If conditions favored the presence of both species, then competitive superiority of either species may inhibit the other from developing. The decreased incubation time for *C. calipes* may create an unsuitable environment for *E. lilaea* . If these species competitively inhibit each other, then the unpredictability of the sequence of succession may prove misleading in a forensic investigation. Studies are needed to compare both species together to see if one species is inhibitory of the other.

Throughout the fourteen days post mortem, 34 species in 4 orders and 20 families were collected (Table 4). Many of these species were incidental and not involved in the decomposition of carrion. The decreased insect activity and low diversity are speculated to be the result of environmental conditions. Adult activity of the blow flies was found to be low on days where fog and clouds created colder temperatures. Payne (1965) found that temperature has more of an influence on insect activity than other environmental factors. The mean, maximum environmental temperature for this area was 20^0C. And, the mean, minimum environmental temperature was 6.5^0C. In this study, core temperatures were not affected by environmental conditions. At the onset of death, the core temperature dropped considerably, then remained relatively stable throughout the fourteen days. According to Connell and Slayter (1977) the tolerance model is indicative of environmental conditions whereby species become more abundant when conditions favor their development. If temperature and environmental conditions were vital to insect presence, then species presence in the successional sequence would be based on these favorable conditions, and the sequence would be virtually unpredictable.

Payne (1965) described 6 stages of decay associated with carrion. Similarly, Early and Goff (1986) described 5 stages of decay in Hawaii. Figure 3 illustrates the similarity of organisms within treatments, and the disjunctions, etc. associated with species composition. Above this graph is the time line and the appropriate stages of decay with successive days. The presence of the "decay" stage, as defined by Early and Goff (1986), is used to define the traumatized carrion in the present study only. In the present study, two stages of decay were achieved over fourteen days in the control and whole-bodied pigs: fresh and bloated. The fresh stage is defined as when the pigs were killed to the first signs of bloating. The fresh stage occurred from the first to the eighth day post mortem. The bloated stage occurs from the first signs of bloating until penetration of the skin by larvae. Within 8 days, bloating had occurred in most of the whole-bodied pigs. In this study, the bloated stage of decay was "skipped" by the traumatized carrion. Instead, by the tenth day post mortem, the exposed organs were all but remnants of blackened tissues in two of the three traumatized pigs. This increased loss of tissue early in the post mortem interval facilitates the need to establish another series of stages associated with traumatized carrion. The non significance of the multivariate ANOVA showed that species composition was not affected by disturbance, but the traumatized carrion did decay at a much faster rate.

The absence of soil in the carrion community was detrimental to the decay process. Of the three treatments, the off-ground pigs were the least affected by blow fly colonization. No soil fauna were found, and no larval migration occurred. Larvae that fell from the mouth due to tissue collapse, or competition, were no longer involved in the decay process. This created very limited areas for resource utilization, and competition for space was very harsh. Bornemissza (1958) concluded that the combination of excretory products by increased numbers of fly larvae and the chemicals produces by decaying flesh changed the chemical nature of the soil. He found that the presence of these chemicals killed the plants directly beneath the carrion. In the present study, the increased decay of the traumatized pigs created an "outline" of each pig. This area was brown and contained increased moisture, and the activity of the fly larvae was heavy. Hence, this study agreed with Bornemissza (1957). In the off-ground pigs, however, plants continued to grow, and the presence of fluids was minimal. The lack of suitable substrate prohibited larvae from utilizing other available resources, thus inhibiting subsequent colonization. Studies of the ecology of "suspended" carrion communities may help to solve the post mortem interval in forensic investigations where soil may be absent due to accidents involving cliffs, trees, and areas where corpses are found in places other than the ground.

The carrion community is a temporary resource utilized by a wide range of species. Carrion feeders consume the flesh, and they, in turn, are consumed by other species. The need to better understand how these species interact is vital for forensic entomology if investigations are to properly determine the post mortem interval. Carrion decay is usually the result of a continuum of change, and the predictability of identifying species composition in the succession of carrion is tedious. The presence of inhibitory species, as well as environmental conditions that favor insect colonization create an ever-present need to study the aspects regarding the ecology of the carrion community and its relationships in solving medicolegal cases.

Literature Cited

Bornemissza, G. F. 1957. An Analysis of Arthropod Succession in Carrion and the Effect of its Decomposition on the Soil Fauna. *Aust J. Zool,* 5: 1-12.

Bray, J. R. and J. T. Curtis, 1957. An Ordination of the Upland Forest Communities in Southern Wisconsin. *Ecol Monogr* , 27 (4) 325-349.

Catts, E. P. 1992. Problems in estimating the Postmortem Interval in Death Investigations. *J Agri Entomol,* 9 (4) : 245-255.

Catts, E. P. and M. L. Goff, 1992. Forensic Entomology in Criminal Investigations. *Ann Rev Ent,* 37: 253-272.

Catts, E. P. and N. H.Haskell, 1990. Entomology and Death: A Procedural Guide. Joyce's Print Shop, Inc. Clemson, South Carolina. 182 pages.

Connell, J. H. and R. O. Slayter, 1977. Mechanisms of Succession in Natural Communities and Their Role in Community Stability and Organization. *Am Nat* , 111: 1119-1144.

Dear, J. P. 1985. A Revision of the New World Chrysomyini. *Rev Bras Zool,* 3: 109-169.

Deonier, C. C. 1940. Carcass Temperatures and Their Relation to Winter Blow Fly Populations and Activity in the Southwest. *J Econ Entom,* 33 (1): 166-170.

Deonier, C. C. and E. F. Knipling, 1940. The Biology of Compsomyiops wheeleri (Hough) and Description of the Larva. *Ann Ent Soc Am* , 33: 578-582.

Early, M. and M. L. Goff, Sept. 1986. Arthropod Succession Patterns in Exposed Carrion on the Island of Oahu, Hawaiian Islands, USA. *J Med Ent,* 23 (5): 520-531.

Field, J. G. and G. Mcfarlane, 1968. Numerical Methods in Marine Ecology: I. A Quantitative "Similarity" Analysis of Rocky Shore Samples in False Bay, South Africa. *Zool Afr,* 3 (2): 119-137.

Hall, David G.,1948. Blowflies of North America. Thomas Say Foundation, Lafayette, Indiana. 477 pages.

Hemphill N, and S. D. Copper, 1983. The Effect of Physical Disturbance on the Relative Abundance of Two Filter-Feeding Insects in a Small Stream. *Oecol* (Berlin), 58: 378-382.

Hewadikaram, K. A. and M. L. Goff, 1991. Effect of Carcass Size on Rate of Decomposition and Arthropod Succession Patterns. *Am J Forensic Med Path,* 12 (3): 235-240.

James, M. T., 1955. The Blowflies of California. University of California Press, Berkeley and Los Angeles. 4 no. 1: 34pages.

Johnson, M. D., 1975. Seasonal and Microseral Variations in the Insect Populations on Carrion. *Am Mid Nat,* 93 (1): 79-90.

Lane, R. P. 1975. An Investigation into Blow fly (Diptera: Calliphoridae) Succession on Corpses. *J Nat Hist,* 9 : 581-588.

Kamal, A. S., 1958. Comparative Study of Thirteen Species of Sarcosaprophagous Calliphoridae and Sarcophagidae (Diptera) I. Bionomics. *Ann Ent Soc Am,* 51: 251-271.

Kneidel, K. A. 1984. Competition and Disturbance in communities of Carrion-Breeding Diptera. *J Anim Ecol,* 53: 849-865.

Knipling, E. F., 1939. A Key For Blow fly Larvae Concerned in Wound and Cutaneous Myiasis. *Ann Ent Soc Am,* 32: 376-383.

Payne, J. A., 1965. A Summer Carrion Study of the Baby Pig *Sus scrofa* Linnaeus. *ECOL,* 46 (5): 592-602.

Pfunter, A. R. 1977. Further Evaluations on Using Blow flies as Indicators of Cadaver Age. Master's Thesis, San Jose State University. 34 pages. (unpublished).

Schoenly, K. and W. Reid, 1987. Dynamics of Heterotrophic Succession in Carrion Arthropod Assemblages: Discrete Seres or a Continuum of Change? *Oecol* (Berlin), 73: 192-202.

Spight, T. M. 1977. Diversity of Shallow-Water Gastropod Communities on Temperate and Tropical Beaches. *Am Nat,* 111 (982): 1077-1097.

Sousa, W. P. 1979. Disturbance in Marine Intertidal Boulder Fields: The Non-Equilibrium Maintenance of Species Diversity. *ECOL,* 60: 1225-1239.

Tabachnick, B. G. and L. S. Fidell, . 1989. Using Multivariate Statistics. Harper Collins Publishers, Inc. New York, N.Y. 746 pages.

Tullis, K. and M. L. Goff, 1987. Arthopod Succession in Exposed Carrion in a Tropical Rain forest on O'ahu Island, Hawaii. *J Med Ent,* 24: 332-339.

Zar, J. H. 1984. Biostatistical Analysis. Prentice-Hall, Inc. Englewood Cliffs, N.J. 718 pages.

Table 1: Multivariate analysis of variance for treatment, time, and location effects for four species of blow fly: *Eucalliphora lilaea* , *Calliphora vomitoria Compsomyiops calipes* , and *Phormia regina* . Treatment contained three levels: trauma, whole-body (Control), and off- ground. Time contained two levels: week one and week two. Location contained two levels: natural orifices and abdominal/traumatized areas.

MANOVA	df	Wilk's	F	P
Treatment	14,12	0.159	1.293	0.33
Location	7,6	0.285	2.153	0.1
Time	7,6	0.096	8.115	0.01
Treat*Location	14,12	0.163	1.269	0.3
Treat*Time	14,12	0.272	0.785	0.6
Location*Time	7,6	0.244	2.659	0.1
Treat*Location *Time	14,12	0.143	1.411	0.2

Table 2: Three-way analysis of variance for treatment, time, and location effects for *Eucalliphora lilaea* . *a priori* comparisons are shown. Treatment contained three levels: trauma, whole-bodied (control), and off-ground. Time had two levels: week one and week two: Location had two levels: natural orifices and abdominal/traumatized areas.

Source	df	SS	MS	F	P
Treatment	2	30.452	15.226	5.759	0.018
a priori comparisons					
Trauma vs. Control & Offground		17.719	17.719	6.702	0.024
Control vs. Offground	1	12.733	12.733	4.816	0.049
Location	1	4.368	4.368	1.652	0.233
Time	1	24.964	24.964	9.442	0.010
Treat*Location	2	4.021	2.010	0.760	0.489
Treat*Time	2	6.419	3.210	1.214	0.331
Location*Time	1	0.071	0.071	0.027	0.873
Treat*Location *Time	2	4.011	2.006	0.759	0.490
Error	12	31.727	2.644		

Table 3: Three-way analysis of variance for treatment, location, and time effects for third instar *Compsomyiops calipes* . a priori comparisons are shown. Treatment levels were: trauma, whole-bodied (control) and off-ground. Time levels were week one and week two. Location levels were natural orifices and abdominal/traumatized areas.

Source	df	SS	MS	F	P
Treatment	2	1.786	0.893	0.372	0.697
Location	1	8.860	8.860	3.694	0.079
Time	1	36.837	36.837	15.356	0.002
Treat*Location	2	3.964	1.982	0.826	0.461
Treat*Time	2	1.786	0.893	0.372	0.697
Location*Time	1	8.860	8.860	3.694	0.079
Treat*Location *Time	2	3.964	1.982	0.826	0.461
Error	12	28.876	2.399		

Table 4: List of species collected from carrion. Stages of decay listed.

ORDER	FAMILY	GENUS/SPECIES	FRESH DAYS 1-7	BLOATED DAYS 8-14
Diptera	Anthomyiidae	*Paregle cinerella*	X	X
	Calliphoridae	*Calliphora vomitoria**	X	X
		*Compsomyiops calipes**	X	X
		*Eucalliphora lilaea**	X	X
		Phaenicia sericata		X
		*Phormia regina**	X	X
	Chloropidae	*Liohippelates robertsoni*	X	X
	Muscidae	*Muscina stabulans*		X
		M. assimilis		X
		Myospila meditabunda	X	
	Phoridae	*Diploneura guadialis*	X	X
		Megaselia sp.	X	X
	Piophilidae	*Piophila casei*	X	X
	Sarcophagidae	Unidentified	X	X
	Scathophagidae	*Scathophaga sterocoraria*	X	X
	Sepsidae	*Enicomira minor*		X
		Sepsis sp.	X	X
	Sphaeroceridae	*Borborillus sordida*		X
		Lotophila atra	X	
		Unidentified		X
Coleoptera				
	Corynetidae	*Necrobia rufipes*	X	X
	Dermestidae	*Dermestes* sp. 1		X
		Dermestes sp. 2		X
		D. lardarius		X
	Histeridae	*Geomysaprinus paeminosus*		X
		Saprinus lugens	X	X
		Xerosaprinus lubricus	X	X
	Hydrophilidae	Unidentified	X	
	Nitidulidae	*Nitidula flavomaculata*	X	
	Silphidae	*Necrophilus hydrophiloides*	X	
		Necrophorus pustulatus nigritis	X	X
	Staphylinidae	*Creophilus maxillosus villosus*	X	
		Unidentified	X	X
Hymenoptera				
	Apidae	*Apis mellifera*	X	
	Ichneumonidae	Unidentified	X	X
	Formicidae	*Iridomyrmex humilis*	X	
		Tapinoma sessile	X	
Acari	Unidentified	Unidentified	X	X
	Ixodidae	*Ixodes pacificus*	X	

* There were only four species of blow fly (family:Calliphoridae) to contain larvae throughout the entire study.

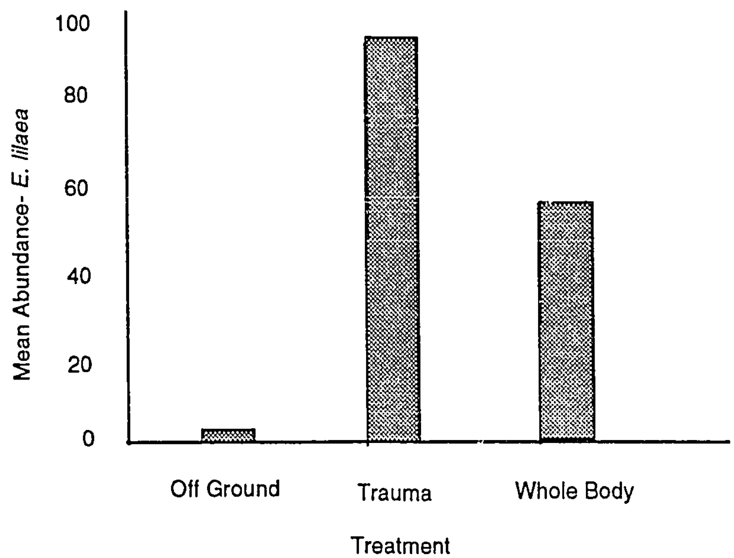

Figure 1: Three -way analysis of variance for treatment showing density of *Eucalliphora lilaea* per volume of pig core mass collected in a 2.5cm X 7.6cm cylinder.

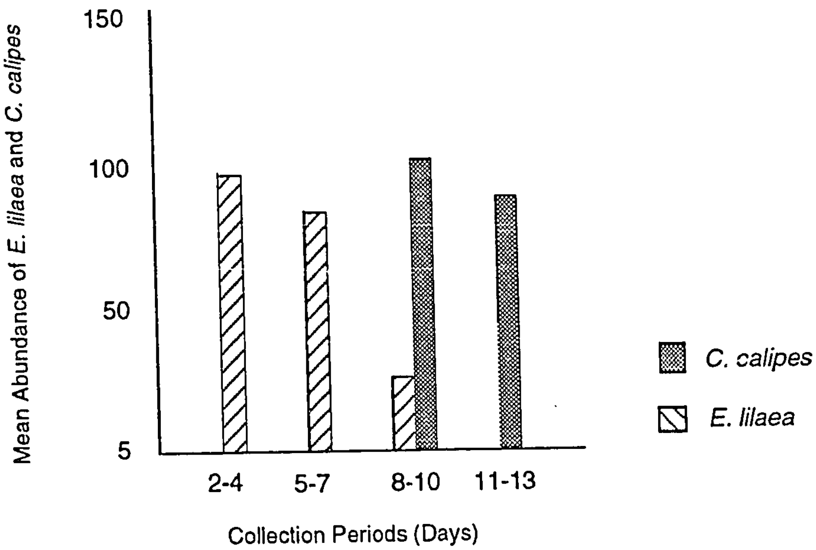

Figure 2: Multivariate analysis of variance for time effect showing mean abundance per 2.5cm X 7.6 cm collection cylinder of *Eucalliphora lilaea* and third instar *Compsomyiops calipes* over four collection periods. Each collection period represents three days of random fly larvae collection. No collections were made on the first and fourteenth days.

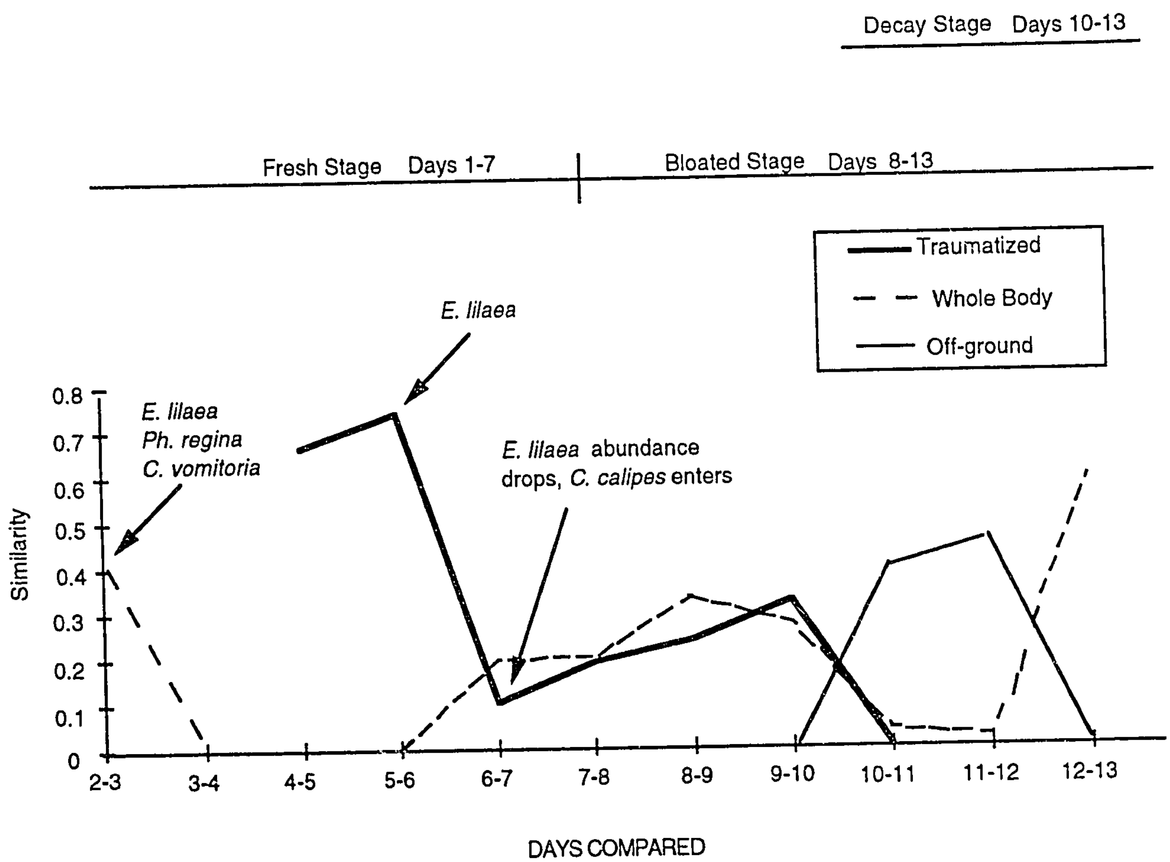

Figure 3: Czechanowski's Quantitative Similarity showing species composition between successive days over time for three treatments: traumatized, whole-body (control), and off-ground.